

ON THE REPTILIAN GENERA *EUPARKERIA* BROOM, AND
MESOSUCHUS WATSON.

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(With Plates II and III.)

The genus *Euparkeria* was founded by Dr. Broom in 1913 for the reception of a small Thecodont reptile from Aliwal North. The type of the genus is an almost complete skeleton including a beautiful skull and lower jaw. In his description of the form Broom differentiated *Euparkeria* from a genus *Mesosuchus*, the two having been grouped previously under the latter name by Watson, who was unaware of the existence of the skull of *Euparkeria*.

The recent acquisition of the famous "Alfred Brown" Collection of fossils by the South African Museum has enabled more development work to be done on the masses of sandstone containing the *Euparkeria* and *Mesosuchus* remains, and the consequent discovery of more skulls and partial skeletons which throw a little more light upon the structure of these two different forms has resulted.

The remains occur in a mass of greenish-grey sandstone which in the main is highly calcareous. The matrix, however, is comparatively easily freed from the bones, which are left clean, and the various sutures of the skulls are clearly displayed. Most of the material recently uncovered belongs to the genus *Euparkeria*, but a fairly complete new skeleton undoubtedly belongs to the interesting Acrodont form *Mesosuchus*. The discovery of a skull of *Euparkeria* lying in close proximity to the pelvis described by Broom as *Browniella africana* has led to the re-examination of the bones of *Browniella*, and the conclusion has been reached that the pelvis and shoulder-girdle said to belong to that form are in reality specimens of *Euparkeria capensis*.

EUPARKERIA CAPENSIS Broom.

In addition to a number of isolated bones the following are the chief specimens of this species, all of which come from a locality known as the Krieffontein Spruit on the Aliwal North Commonage, and are of Upper Beaufort age. (The numbers in brackets refer to the South African Museum catalogue.)

Specimen 1 (5867).—The type. Consists of skull, lower jaw, shoulder-girdle, cervical and dorsal vertebrae, right fore-limb without hand, abdominal ribs, pelvis, and most of the left hind limb. Associated with this by Broom is another dentary, and a complete pes.

Specimen 2 (6047).—A complete skull and lower jaw, humerus, pelvis and shoulder-girdle (described previously as *Browniella africana*), femur in articulation with pelvis, vertebrae, ribs, abdominal ribs.

Specimen 3 (6048).—Skull, of which the bones are disarticulated and scattered but not broken, pelvis, of which the ilium was figured by Broom ('Proc. Zool. Soc.,' 1913, pl. lxxviii, fig. 18), hind limb, some vertebrae and ribs.

Specimen 4.—Dorsal vertebrae, pelvis (ilium figured by Broom, 'Proc. Zool. Soc.,' 1913, pl. lxxviii, fig. 17), hind limb, coracoids and interclavicle.

Specimen 5.—Disarticulated skull, scapula, fore limb, hind limb, and some vertebrae.

Specimen 6.—A portion of the antorbital part of the skull and lower jaw showing a little of the palate.

Skull.—Specimen No. 2 contains an almost complete skull and lower jaw, of which some of the bones are slightly displaced. Pressure has cleaved the skull along the middle line except at the snout, and has crushed the left side so that the left frontal is vertical and the left nasal is horizontal, but at a lower level than its neighbour. The left ramus of the mandible is in its correct position but the right ramus has been displaced. All the sutures are beautifully shown, but accurate measurements are not possible, save those of each separate bone.

The skull is undoubtedly of the same species as the type and almost of the same size; but it displays one or two features which are not shown by the type-specimen.

The front part of the left premaxilla is as conjectured by Broom, being a slender pillar of bone bounding the front of the large nostril and meeting the nasal above it. The postnarial portion of the bone is seen to overlap the descending part of the nasal on the outside, and the suture between the two is somewhat different from that in Broom's figure. The premaxillary teeth are not seen.

The nasal-maxillary articulation is longer than in the type; the frontoparietal and fronto-postfrontal sutures are jagged; the maxilla and jugal are supplied with a number of small foramina, mostly passing forwards into the bones; and the distal end of the quadrate is broader than in the figures given. Apart from these facts nothing can be added to Broom's description, with which this skull closely agrees. No sclerotic plates, however, are preserved.

The lower jaw shows several features which are not displayed by the type. The dentary forms the anterior half of the ramus and forms the

symphysis, articulating posteriorly with the surangular and angular. The lower view of the ramus shows a splenial lying within the dentary forming part of the lower border of the jaw, passing back almost to the level of the front of the external mandibular foramen but not reaching the symphysis anteriorly. Lying wedged between the lower half of the dentary and the posterior half of the splenial is the anterior prolongation of the angular. The angular forms the lower border of the external mandibular foramen, and the lower border of most of the hinder half of the ramus. The surangular lies dorsal to the angular, and extends from the dentary to the articular. Just anterior to the articular it has a fairly large nutritive foramen; above the external mandibular foramen and just below the dorsal edge of the bone is a well-defined groove leading backwards to a small foramen; and the upper edge of the bone is thickened to form a small flange. Lying below the posterior half of the surangular and apparently passing between it and the angular is a slight splint-bone which I take to be a prearticular. It is small. The limits of the articular are not well defined. At the actual articular surface it is bounded outwardly by the surangular, which passes back to lie outside the postarticular process. The articular surface is shallowly concave and broad for the reception of the broadened quadrate. I can see no evidence of a coronoid.

The teeth, at least in the lower jaw, are serrated on their anterior and posterior borders, the posterior serrations being much the coarser of the two sets. I can see no definite trace of anterior serrations in the upper jaw, and some teeth are certainly without.

Specimen No. 6 is of interest as showing a small fragment of the palate in association with part of the side of a skull. The specimen is somewhat unsatisfactory, but it is possible to identify the elements present. Most of the left orbital and preorbital region is preserved, and the front of the left ramus of the lower jaw; the stone containing the specimen has split almost longitudinally, so that the inner face of the maxilla is seen on one piece and the outer side of the jugal on the counterpiece. Comparison of the lower jaw with the type shows that the specimen is not quite full grown. The lower jaw shows definitely that the splenial plays no part in the symphysis. The only real point of interest in the specimen is the evidence of small teeth on the palate. These are short, blunt, smallish teeth exposed in a row of four or five on a bone, which apparently articulates latero-anteriorly with the hinder part of the maxilla. The teeth begin behind the level of the orbit and are placed in the long axis of the skull. It is probable that they are borne by the pterygoid, as in the somewhat earlier form *Proterosuchus fergusi*.

It should be noted that there is in the collection another fragment showing a portion of the maxilla with two thecodont teeth, serrated posteriorly; and associated with it a bone of the palate carrying a row of eight

short pointed slightly backwardly-curved small teeth, apparently unserrate. It seems indisputable, therefore, that *Euparkeria* had palatal teeth and was thus more primitive than *Ornithosuchus*—a conclusion strengthened by the discovery of the prearticular in the lower jaw of the South African form.

Humerus.—The humerus of the type is only displayed in its outer aspect; but a complete left humerus has been isolated from skeleton No. 2. The greatest length of the bone is 45 mm., its maximum proximal width 20 mm., and its distal width 16 mm. The shaft is very slender, but the bone expands considerably at the ends, especially proximally. The lower end of the deltoid crest is only 14 mm. from the proximal edge of the bone, and the crest thus lies high up as in *Ornithosuchus*. The inner face of the proximal end is mostly flat, but is slightly concave laterally. The distal condyles are separated by a basin-like depression. There is no entepicondylar foramen.

Ilium.—The specimen from which Broom figured the imperfect ilium (1913, fig. 18) also contains a perfect right ilium which has been fully developed. The whole bone is 20 mm. high and the iliac crest 28 mm. long. The acetabulum is large and closed and there is a very pronounced supra-acetabular crest. The height of the acetabular portion of the bone is 13 mm. The anterior spine of the crest is short and bluntly rounded, the posterior spine long. The acetabular crest is continued on to the pre-acetabular process, but not to the post-acetabular process. The lateral face of the upper portion of the bone is strongly supplied with ridges running at right angles to the upper border, especially in the anterior portion.

Femur.—Directly associated with the pelvis figured by Broom as that of *Browniella africana* I have discovered a left femur. The head of the bone lies just under the ischium and the bone is at right angles to the plane of the ischium. It is closely similar to that of *Euparkeria capensis*, having a length of 59 mm., the femur of *Browniella* being 74 mm. long; and this coupled with the fact that a skull and lower jaw of *Euparkeria* was found in the sand-stone lying directly under the same pelvis opens up the question of the identity of the pelvis figured by Broom.

Broom has referred to the differences which exist between this pelvis and that of the type of *Euparkeria*. "The ischium differs in shape in being constricted near its middle, and the pubis, besides being much broader and stouter, differs in having only a single pubic foramen." Further development and a careful examination of the "*Browniella*" pelvis seem to show that these differences were rather too strongly accentuated. Ilium, pubis and ischium are certainly larger than those of the other specimens of *Euparkeria* examined; but their relative sizes are apparently the same. The constriction of the ischial plate does not exist—the appearance of constriction is due to a broken edge of the bone, the true shape being evident on the matrix beneath. The ilium is of exactly the same type as in

Euparkeria. There is some doubt as to the value of the other point of difference mentioned. None of the pubes of *Euparkeria* are quite entire, but in at least one there is no evidence of a second pubic foramen.

In view, therefore, of the general similarity of the pelvis to that of *Euparkeria*, its articulation with a typical *Euparkeria* femur and its close association with an undoubted *Euparkeria* skull and lower jaw, it must be concluded that this pelvis is a large girdle of *Euparkeria capensis*, its difference in size from the type being probably due to differences of sex. It is worthy of note that Watson found similar differences in two skeletons of *Procolophon*, of which he writes—"The male and female skeletons are of exactly the same length, as are their skulls. The dentition is quite similar in the two specimens, and I think there is not the slightest doubt that they belong to the same species. The female skeleton is, however, much more lightly built, having narrower and more slender limb-girdles, and limbs which are less than three-quarters as long as those of the male skeleton and much less robust. Mr. Boulenger tells me that differences of this kind often distinguish the sexes in living lizards, and I think it is extremely probable that the same reason accounts for the difference between my two skeletons." In *Euparkeria* the limb bones are more closely similar in the two sexes than in *Procolophon*, but there is a marked difference in the size and strength of the pelvis and shoulder-girdle.

BROWNIELLA AFRICANA Br.

In view of the foregoing discussion, I take as the type of *Browniella* an isolated femur, longer than that of *Euparkeria* and somewhat less curved. The resemblances between the two are great, but from the figures it will be seen that in *Browniella* the trochanter is considerably straighter. The distal end is less broadened than in *Euparkeria*.

MESOSUCHUS BROWNI Watson.

The fortunate discovery of a second specimen of this interesting form in the Brown collection enables certain new facts to be added to our knowledge of it. The specimen consists of a fairly complete articulated skeleton lacking the skull—of which only a portion of a maxilla is preserved—of which the pelvis, hind limb and fore limb have been developed. The type of the genus is a somewhat unsatisfactory specimen; but this second piece agrees very closely with the type in size and specific characters. It is unfortunate that the skull is not preserved.

The fragment of maxilla is about 30 mm. long and carries nine blunt round acrodont teeth, which are not arranged in a single row but somewhat irregularly.

Of the fore limb the parts preserved are the distal end of the humerus,

the radius and ulna and the hand. The distal end of the humerus is 17 mm. broad. It has two distinct condyles with a broad shallow depression between them. There are no epicondylar foramina.

The radius has a length of 33 mm., and consists of a thin shaft expanding at each end to a width of about 7 mm. The distal end is cup-shaped for the reception of the radiale, which is closely applied to the bone.

The ulna is not fully exposed. Its length may have been slightly less than that of the radius. The bones of the forearm are crossed, so that the distal end of the ulna lies on the opposite side of the radius to the proximal end.

The bony carpus consists of six elements—two fairly large proximal ones and four smaller distal ones. The largest bone articulates closely with the radius and is irregularly quadrangular in section. The other proximal element lies at the distal lateral corner of the radiale, well separated from the ulna. Its lateral face is excavate as if for the reception of another, possibly cartilaginous, element. Of the distal elements the second is small, the first and third are equal to one another in size, and the fourth slightly larger. The first, second and third articulate with metacarpals I, II and III; the fourth with metacarpal IV and partly with metacarpal V, which also articulates apparently with the outer proximal element. The metacarpals have the following lengths: I, 5 mm.; II, 10 mm.; III, 12 mm.; IV, 13.5 mm.; V, 6 mm. The digital formula is 2, 3, 4, 5, 3 (the claw of the fifth finger is displaced), and the fingers (excluding the metacarpals) have the following lengths: 1, 10 mm.; 2, 13 mm.; 3, 16 mm.; 4, 18 mm.; 5, 8 mm. The claws are comparatively long and pointed. All the fingers are slender. The fore foot is smaller than the hind foot.

The whole pelvis is preserved, practically undistorted. The left ilium is entire. As Broom has pointed out, it differs considerably from that of *Euparkeria* and resembles much more closely that of *Howesia*. The maximum vertical height of the bone is 28 mm., the height above the supra-acetabular ridge 16 mm. The length of the dorsal edge is 25 mm. The posterior extension of the crest is much less than in *Euparkeria*. The acetabulum is closed.

The ischium is a plate-like bone meeting its neighbour in a nearly complete symphysis, and sloping downwards and inwards from the acetabulum to form a very obtuse-angled depression. It is considerably shorter than that of *Euparkeria*. Its greatest length cannot have been more than 27 mm., its anterior width 13 mm. The pubis is 21 mm. broad posteriorly. It is plate-like, with the anterior half of the plate bent nearly at right angles to the posterior half, so that the two pubes together form a nearly vertical wall of bone. The anterior edges are considerably thickened laterally. The posterior edges of the bone are not quite straight, so that the articulation with the ischia was not complete, a lozenge-shaped area being left

uncovered by bone in the centre of the pelvic basin. The pubis has one pubic foramen. The bending of the bone is greater than in *Howesia* and equal to that of *Euparkeria*.

The femur is a short stout bone 50 mm. long, very different from that of *Euparkeria*. It is bent in a slight double curve. The head must have been cartilaginous, as the proximal end of the bone is excavate and finely rugose, approximating in shape to that of *Howesia*. There was a strong high trochanter at the proximal fifth of the bone. The bone differs from the femur of *Howesia* in being less expanded at the distal end and in having a stronger curve.

The tibia is 49 mm. long, the fibula 45 mm. The proximal surface of the tibia has a maximum width of 12 mm., the shaft being 5 mm. thick. The fibula is a much more slender bone with a somewhat expanded distal end.

The tarsus of the right side is seen from the plantar side, and is slightly displaced. In the proximal series there are three bones. A large bone, obviously formed by the fusion of two, lies directly opposite the distal ends of the lower bones of the leg. It is 14 mm. at its widest and has a maximum length of 7 mm. Lateral to it and apparently lying partly above it is a bone which has only a small triangular plantar face. External to this and partly articulating with the first is another large bone whose inner edge is raised and whose under-surface is saddle-shaped. The dimensions of this bone are 11 mm. by 8 mm. In the distal row four tarsalia are seen, of which the fourth is the largest. The metatarsals are not fully displayed, with the exception of the first and fifth. The first is a short stout bone; the fifth is remarkably similar to that of *Howesia*. The digital formula is not obtainable.

There can be little doubt that in the structure of the girdles and limbs *Mesosuchus* and *Howesia* are closely allied forms. The pelvis is very similar in the two genera and so is the general form of the limb-bones, while the similarity in the fifth metatarsal is very striking. The manus is not known in *Howesia*, and its interpretation in *Mesosuchus* is not beyond doubt. Much of the carpus was undoubtedly cartilaginous. There were certainly four distal carpalia. I have interpreted the other two bones as radiale and ulnare; the absence of a bony intermedium is strange, but there is room for it between the two proximal bones of the carpus. There were almost certainly cartilaginous centralia, and the lateral surface of the supposed ulnare is excavate as if for articulation with a cartilaginous pisiforme. The digital formula of the hand is primitive.

The structure of the tarsus is fairly clear, although the whole foot has been turned at an angle to the leg. The large bone which articulates with the tibia and fibula is taken to be a fused centrale and tibiale; lateral to this and just possibly fused with it (although a suture seems undoubted on the

plantar side) is the intermedium. Lateral to this is the large fibiale with a pronounced heel. This structure differs from that of *Howesia* in the fusion of the tibiale and centrale. Such a fusion is paralleled in stage Q of *Sphenodon*; and a further fusion with the intermedium is seen in *Procolophon*. In the rest of the foot *Howesia* and *Mesosuchus* agree. A specimen from Burghersdorp (S.A. Mus. Cat. No. 5861) collected by Dr. du Toit shows the fingers and toes of a species of either *Howesia* or *Mesosuchus*. The fifth metatarsal is of exactly the same type as in those genera, and the digital formula of the pes is 2, 3, 4, 5, 3. The third metatarsal is the longest.

The femur in the Howesiidae differs from that of the Pseudosuchia such as *Euparkeria* and approximates more closely to that of *Erythrosuchus*, but in the latter the large medial trochanter is not terminal. The forms agree with *Erythrosuchus*, too, in the sudden bending down of the anterior portion of the pubis; but the ilium lacks the posterior prolongation seen in both *Erythrosuchus* and *Euparkeria*.

EXPLANATION OF PLATES II AND III.

FIG.

PLATE II.

1. *Euparkeria capensis*. Outer view of left dentary of Specimen No. 2.
2. *Euparkeria capensis*. Lower view of same.
3. *Euparkeria capensis*. Lateral view of humerus of Specimen No. 2.
4. *Euparkeria capensis*. Medio-anterior view of same.
5. *Euparkeria capensis*. Femur.
6. *Browniella africana*. Femur.
7. *Euparkeria capensis*. Pelvis of Specimen No. 2.
8. *Euparkeria capensis*. Right ilium of Specimen No. 3.

PLATE III.

Mesosuchus browni, Watson.

1. Left ilium.
2. Pelvis from below.
3. Proximal end of femur.
4. Femur.
5. Fore limb, showing carpus.
6. Hind limb, showing tarsus.
7. True view of metatarsal V.